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SHORTER ARTICLES AND DISCUSSION

VARIABILITY UNDER INBREEDING AND CROSS-BREEDING

An unusually thoughtful and suggestive discussion of evolutionary problems is contained in Professor Walton's paper on "variability and amphimixis" published in the November, 1915, number of this journal. But the paper is in some danger of neglect because the conclusions reached are apparently so revolutionary that to a casual reader they may seem freakish. Yet it will be seen by one who reads the paper more carefully that the radical character of its conclusions is due in part to the fact that certain familiar ideas are here viewed at a new angle. Nevertheless the new point of view has, it seems to me, to some extent, caused the author loss of perspective in relation to some of the phenomena which he discusses, for which reason further consideration of them may be profitable.

The occasion of Walton's discussion was a biometric study which he made of two sorts of zygospores produced by *Spirogyra inflata,* one sort produced by union of cells in the same filament (called by him "close fertilization"), the other by the union of cells in different filaments (called "cross fertilization"). Zygospores of the former sort ("close fertilized") were found to be on the average larger and more variable than those of the latter sort, *contrary to the prevailing idea that cross fertilization leads to increased variability.* It may however be questioned whether Walton's material is such as to throw new light on this question, for it is by no means certain that cells of *Spirogyra* which unite in lateral conjugation are the exact equivalents morphologically and physiologically of those which unite in scalariform conjugation. It is conceivable that zygospores formed in lateral conjugation may be larger and more variable because the cells which gave rise to them were as a group larger and more variable. It is conceivable that cells which resort to scalariform conjugation are not such as can satisfy their physiological demands for conjugation by uniting with a sister-cell in the same filament. For it is known that in many plants sexual union occurs only as a last resort, when conditions are unfavorable for further continuance of the organism either by vegetative reproduction or even by parthenogenesis.[1] But whether or not Walton's own observations are considered pertinent, the question which it leads him to consider is one of profound evolutionary significance—does cross fertilization (as compared with close fertilization) tend to produce greater or less variability.

In parts of his discussion Walton fails to keep clearly in view distinctions, which he nevertheless recognizes, between the respective variabilities of F_1, F_2 and mixed populations. The fact has been known since the days of the early plant hybridizers, and is expressed clearly in one of Focke's laws of hybridization that the first generation (F_1) offspring of a hybrid cross are not, as a rule, more variable than the more variable parent race. In other words the generalization which Walton attacks, that crossing produces variability, is not commonly, if at all, held by biologists to apply to F_1 populations but only to the conditions obtaining in subsequent generations. But Walton's own observations are made exclusively upon F_1 zygotes. Supposing his two classes of zygotes to be morphological and physiological equivalents of each other (which, however, may reasonably be questioned) there was no ground for expecting one sort to be more variable than the other, so far as existing knowledge of the effects of inbreeding and cross-breeding is concerned.

Walton cites two experimental investigations, in support of his own observations on *Spirogyra,* to show that close fertilization produces greater variability than cross fertilization, viz., that of Jennings on *Paramecium* and that of Barrows and myself on *Drosophila.* But neither of these investigations deals with the same sort of cases as Walton's. Jennings is comparing the variability of conjugants with that of non-conjugants. This is a case where sexual is contrasted with asexual reproduction and is in no way comparable with a case in which the effects of cross and close fertilization are compared with each other. I quite agree with Walton's conclusion that the results are statistically considered far from conclusive, and would add that they are quite aside from the question which Walton is considering. Barrow's comparisons were made between *single lines* of *Drosophila* inbred (brother with sister) for from 30 to 61 generations and a culture derived from two original pairs of

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[1] See Coulter, 1914, "The Evolution of Sex in Plants."

Drosophila the descendants of each pair being allowed to interbreed freely. As to the results we said (p. 776):

> These experiments show no appreciable effect of inbreeding (on variability). In every case the brood reared under the best and the most uniform conditions has the highest average number of teeth (in the sex-comb), irrespective of whether or not inbred. The same may be said of variation in size. Inbreeding has diminished neither the average size nor the variability in size.

Walton considers these conclusions justified by our statistical constants in the case of the sex-comb, but believes that a significant difference is observed in length of tibia, which we found to be both greater and less variable in the culture not inbred. He criticizes our failure to calculate coefficients of variation for tibia length (as we had done for sex-comb) and upon calculating such coefficients finds the greater variability of the inbred lots significant. But the same difference in variability was indicated by the standard deviations (which we gave) and the calculation of the coefficient of variation adds nothing to the force of the demonstration. We considered then and still consider the differences observed sufficiently accounted for by external conditions, *i. e.,* we considered them purely phenotypic. We showed that length of tibia is greatest and its variability least when food and temperature conditions are best. The difference between two inbred races (*M* and *N*) inbred practically the same number of generations (viz., 31 and 30, respectively) but treated very differently as regards food, was found to be several times greater than the difference between the inbred culture *M* and the not-inbred culture *X*. Hence it is not probable that the inbreeding had anything to do with the differences found in variability.

It is difficult to understand how on any theory of heredity inbreeding could be expected to *increase variability* within a single inbred line, such as one of our inbred cultures of *Drosophila.* On a Mendelian theory it would be expected that inbreeding, brother with sister, for a large number of generations (61 in our *A* series) would result in the production of a number of homozygous lines, each of which by itself would be *entirely devoid* of variability, except that due to environmental agencies. If all the possible derived lines descended from a pair under inbreeding were combined into one mass of material, it would seem probable, on a Mendelian theory, that if any genotypic variations had occurred, this material would show greater variability than the ancestral race before inbreeding began. This, I take it, is the point which Walton has in mind when he asserts that inbreeding has a tendency to increase variability. But this is very different from the condition to be expected in any *single line* considered separately, as in one of our inbred lines of *Drosophila.* Such a line should be *less variable* than the population from which it arose, provided that population contained any genotypic variations whatever!

The question is decidedly worthy of consideration, which Walton's paper suggests, is evolution more rapid in a self-fertilizing or habitually close fertilizing population on one hand or in a habitually cross fertilizing population on the other hand. The importance of the question is not lessened by the fact that Walton has brought into the discussion material wholly irrelevant, including his own observations on the zygospores of *Spirogyra* and the observations of Jennings on *Paramecium* and Barrows on *Drosophila.* But the work of Hayes on the variability of pure races of tobacco and of their hybrids, which Walton cites, does bear directly on this question. By combining the observations on the parent races into one mass of data and treating this statistically, Walton has shown that self-fertilizing lines *mixed together* would form a population more variable as regards number of leaves and height of plant than the population produced by cross-breeding of these same lines. Hayes's observations verify Focke's law already cited, that the variability of F_1 does not exceed that of the more variable parent race, but that F_2 shows increased variability. Theoretically F_2 should show the *maximum* variability. Walton's figures indicate clearly that this maximum variability under cross-breeding is *less* than the variability of a mixture of the two inbred races and consequently that continuous self fertilization within a mixed population will produce a more variable population than will result from continuous cross fertilization. This is an important generalization which demonstrably will hold good in all cases in which "intermediate" or "blending" inheritance occurs. It would not hold good for cases in which completely dominant and quantitatively invariable Mendelian factors are concerned, but it is doubtful whether such cases occur, as I have elsewhere tried to show. It is the great variability of self fertilizing populations and the stability of variations arising under self fertilization (since no variations will be "swamped by crossing'' in a self fertilizing population) that allow of the formation and perpetuation of ''little species,'' side by side and yet quite distinct, within highly variable taxonomic species such as the dandelion. These same characteristics of self fertilizing populations furnish much of the material which plant breeders use. Following Vilmorin, they find it necessary only to *isolate* and propagate by themselves the variations which spontaneously arise. The task of the breeder who is dealing with a continually cross-breeding organism is much more complex. He often finds it necessary *first to inbreed* his stock, in order to learn what potential variations it contains, or, if one prefers so to express it, in order to induce variability, though this form of statement is not strictly accurate. Such inbreeding of a naturally cross-breeding organism often causes temporary loss of vigor, as notably in the case of maize, and frequently in domestic animals. But when the desired variations have been isolated, vigor can usually be recovered by increasing the stock to such an extent that matings become possible within the race and yet not involving union of closely related individuals.

Notwithstanding the utility of inbreeding in securing variations, there are important sources of variability which are found in cross-breeding alone. Supposing that under inbreeding variation has already occurred in different directions and the original condition has been wholly lost, it is often possible to recover it again by crossing. This is the familiar phenomenon of reversion upon crossing. It is also possible by crossing to combine in one race variations which have occurred separately in different races, a thing which would be impossible under continuous inbreeding. But a certain amount of inbreeding must usually in such cases follow up the cross-breeding in order to isolate and make secure the combinations desired.

It is not wise, therefore, unduly to exalt either inbreeding or cross-breeding as evolutionary processes or tools of the breeder. Each has its utility at the proper time and place. They are like pick and shovel, each supplementing the work of the other.

The question is worth considering in this connection—what effect will inbreeding and cross-breeding respectively have on the variability of single characters. This is a question to which I have given considerable attention for several years and the answer to it is, I think, becoming clear. A single character which Mendelizes has its variability increased by crossing. Some explain this as due to actual modification of the unit character through crossing, others as due to the introduction of modifying factors by means of the cross. Whichever view is adopted, the fact is perfectly clear that modification of single Mendelizing characters occurs in cross-breeding. Under continuous inbreeding we should expect that single Mendelizing characters (within single lines but not within an entire inbred population) would attain a condition as devoid of variability as it is possible for them to attain and observation confirms this expectation.

As regards characters which "blend" in heredity, these are not inherited as single characters; they do not Mendelize in the ordinary acceptation of the term. The characters of the respective parent races *disappear* in the cross, being replaced by a common intermediate condition or blend. This blend persists into the F_2 and later generations but with a certain amount of variability which is at a maximum in F_2 and beyond that point tends to disappear in the absence of any special selection. It points to imperfection of the blending process or, in the view of those who prefer a Mendelian terminology for such cases, it points to *plurality* of factors determining the character. All the cases with which Walton has dealt in the paper under review are cases of *blending* inheritance and as regards them it is true, as already indicated, that continuous inbreeding tends to the production of a *more varied population* (but not of more variable separate lines) whereas cross-breeding tends to produce a *less variable population* (devoid of differences between families) but nevertheless a population more variable than the single lines of a self fertilizing or constantly inbred population.

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